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The chronology and frequency of a stress marker (linear enamel hypoplasia) in recent and archaeological populations of *Sus scrofa* in north-west Europe, and the effects of early domestication

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Abstract

Linear enamel hypoplasia (LEH), a deficiency in enamel formation visible on mammal tooth crowns, can be used as a retrospective indicator of physiological stress and developmental health in humans and animals. In this first study, for north-western Europe, the condition has been recorded from prehistoric (mesolithic) and recent populations of wild boar, and from domestic pigs belonging to early farming (neolithic) communities. It was possible to show that LEH occurs in recent and ancient populations of wild boar from north-west Europe, and that the occurrence of the condition can be explained by the same events within the animal's life (birth, weaning, winter starvation) as has been previously suggested for archaeological domestic pig samples. The frequency of LEH is consistently low within all ancient and recent populations of wild boar studied, a remarkable observation given the pronounced differences in the living conditions of these two diachronically well-separated groups, mainly linked with the increasing human pressure on recent populations of wild animals. Early domestic samples generally show high LEH frequencies, although considerable variation exists between the samples. It is suggested that these high frequencies are, in general, the result of domestication, while the variation could be related to differences in early husbandry. The observation of LEH, therefore, provides a valuable tool for studying the history of animal domestication.

Key words: wild boar, domestic pig, *Sus scrofa*, north-west Europe, prehistoric husbandry, dental defects

INTRODUCTION

Mammal teeth can provide many clues to an individual's living conditions, and certain developmental defects of teeth have been used as a retrospective way of studying physiological stress in mammal populations. Linear enamel hypoplasia (LEH) is a deficiency in enamel thickness occurring during tooth crown formation, typically visible on a tooth's surface as one or more grooves or lines (Colyer, 1936) (Fig. 1). The condition is generally caused by developmental stress (Sarnat & Moss, 1985), the causes of which can be varied in nature but nutritional deficiencies are certainly an important factor. Within anthropological studies of archaeological and recent material, the analysis of LEH has successfully been used to assess the general health status of human populations (Goodman *et al*., 1988). In the present study for the first time, the same analysis is applied to modern wild boar *Sus scrofa*, and to prehistoric wild and domesticated pigs *Sus scrofa* f. *domestica* from north-western Europe.

The methodology for recording LEH on pig molars from the lower jaw has previously been published (Dobney & Ervynck, 1998; revised by Dobney, Ervynck & La Ferla, 2002). Subsequently, it has been proven using archaeological material that LEH is not a rare or randomly occurring event in domestic pigs. In fact, for five different assemblages, it was possible to construct a chronology of physiological stress events, which explained why, generally, LEH is always present at the same heights on the molar crowns. It was proposed that birth and weaning are the direct causal agents of two discrete peaks in the height distribution of LEH on the first permanent molar (M_1), whilst a period of under-nutrition encountered during the first winter of the animal's life is thought to be the main causal factor for the occurrence of the single distinct LEH peak noted on the M_2. A broad peak on the M_3 is similarly interpreted, i.e. as reflecting the animal's second winter. This chronology could be consistently applied to all five archaeological collections studied (Dobney & Ervynck, 2000), and this pattern has now been further corroborated by studies on additional

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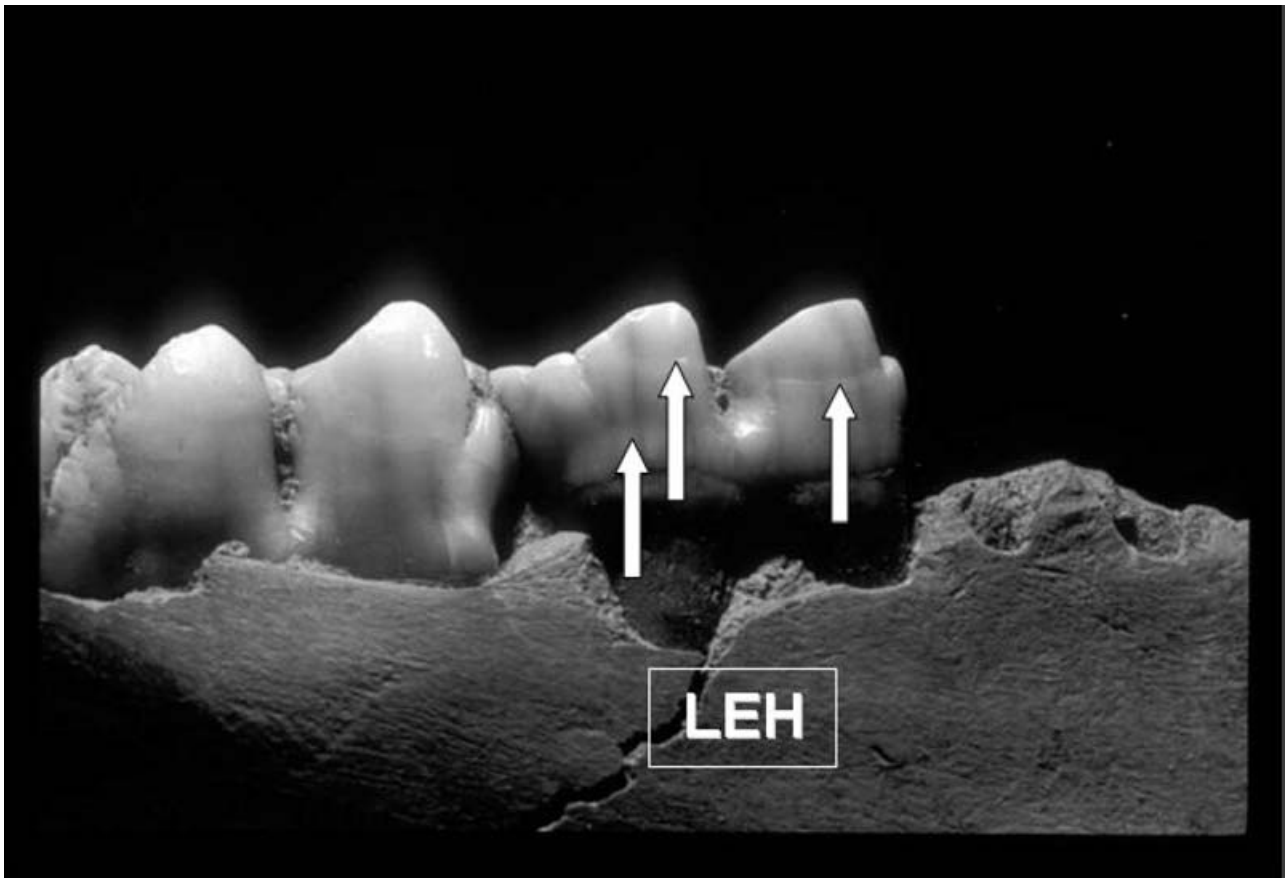

Fig. 1. Linear enamel hypoplasias (LEH, arrowed) on the lingual surface of mandibular second molar of an archaeological pig *Sus scrofa* (Ename, Belgium).

archaeological assemblages (Dobney *et al*., 2002). Finally, it was shown that the link established between the patterns of LEH and the developmental physiology of the domestic pig allows inferences to be made about former environmental conditions and husbandry practices. From an analysis of the five assemblages of pig mandibles used to establish the LEH chronology, it was suggested that degradation of forest environment through the Middle Ages was responsible for an increase in the frequency of LEH in domestic pigs. Conversely, a supposed shift in pig husbandry, from forest herding to rearing in (semi-)confinement, was put forward as the cause of a significant decrease in the occurrence of the tooth defect towards the end of the Middle Ages (Ervynck & Dobney, 1999). In general, therefore, the observation of LEH shows much potential in being a valuable tool in archaeozoological interpretation.

The aim of this paper is to establish the chronological patterns and frequency of LEH in recent wild boar populations in north-western Europe to evaluate whether (and if so, how) these differ from those previously published for ancient domestic pigs. Secondly, a comparison is made with prehistoric wild boar material to see whether the ecology of wild boar has changed through time regarding this phenomenon. Lastly, material of early domesticated pigs (from the north-west European Neolithic) is introduced into the analysis with the aim of establishing a possible signature of early human interference.

MATERIAL AND METHODS

Linear enamel hyperplasia was recorded from the permanent molars of the mandibles of museum specimens representing recent wild boar populations from France, Germany, Switzerland and Poland (Table 1). Where information was available, zoo specimens and hybrids have been excluded from the analysis. Material from prehistoric wild boar has also been collected from mesolithic archaeological contexts (*c*. 10 500–4000 BC in calibrated radiocarbon years) (Tables 2 & 3), i.e. from the period during which (as far as we know) domestic pigs did not yet occur in north-western Europe. Early domestic pigs are represented by material from several neolithic archaeological sites (c. 5500–2000 cal BC) (Table 2). Although the neolithic was the period during which animal husbandry was introduced or developed in north-west Europe for the first time, hunting remained an important economic basis for certain sites or cultures (Aaris-Sørensen, 1988; Schibler, Jacomet *et al*., 1997). As a result, remains of both wild and domestic pigs could also be expected to be present within such sites, which, given the sometimes small morphological differences between

Table 1. Collections of recent wild boar *Sus scrofa* mandibles studied

Country	Collection	No. of M_1	No. of M_2	No. of M_3
Germany	Natural History Museums of Bern, Berlin, University of Hildesheim and the Smithsonian Institution, Washington, DC	64	62	55
France	Natural History Museums of Paris, Geneva, Bern and Berlin	53	51	37
Switzerland	Natural History Museums of Geneva, Bern and Berlin	56	55	31
Poland	Natural History Museum of Berlin	76	72	50

Table 2. Collections of prehistoric (mesolithic) wild boar *Sus scrofa* and of prehistoric (neolithic) domestic pig studied. Early, middle or late refer to the local chronologies, which can differ markedly between regions within Europe. Neolithic material might include wild boar specimens (see text). Geol, Institute for Historical Geology and Palaeontology, University of Copenhagen; ZMUC, Zoological Museum, University of Copenhagen; BLDAM, Brandenburgisches Landesamt für Denkmalpflege und Archäologisches Landesmuseum; ROB, Rijksdienst voor het Oudheidkundig Bodemonderzoek; Hist, Statens Historiska Museum, Stockholm; NMBB, Naturhistorisches Museum der Burgermeinde Bern; KAZ, Kantonsarchaeologie Zürich; AATH, Amt für Archaeologie Thurgau; Stock & Got, Stockholm University, Department of Archaeology and Gotland University College; LVH, Landesmuseum für Vorgeschichte Halle

Country	Location	Period	Dating	Collection	References
Denmark	Agernæs	Mesolithic	5300–4000 BC	Geol	Noe-Nygaard & Richter, in press
Denmark	Bloksbjerg	Mesolithic	5300–4000 BC	ZMUC	Johansen, 2000
Denmark	Flynderhage	Mesolithic	5300–4000 BC	ZMUC	Johansen, 2000
Denmark	Holmegaard	Mesolithic	8200–6500 BC	ZMUC	Johansen, 2000
Denmark	Kongemose	Mesolithic	6500–5400 BC	Geol	Johansen, 2000
Denmark	Lundby	Mesolithic	8200–6500 BC	ZMUC	Johansen, 2000
Denmark	Mullerup	Mesolithic	8200–6500 BC	ZMUC	Johansen, 2000
Denmark	Niva	Mesolithic	5300–4000 BC	ZMUC	Johansen, 2000
Denmark	Norslund	Mesolithic	5300–4000 BC	ZMUC	Johansen, 2000
Denmark	Sludegard	Mesolithic	5300–4000 BC	Geol	Noe-Nygaard & Richter, 1990
Denmark	Svaerdborg	Mesolithic	8200–6500 BC	ZMUC	Johansen, 2000
France	Noyen-sur-Seine	Mesolithic	No radiocarbon dates	NHMP	Marinval-Vigne *et al.*, 1989
Germany	Friesack	Mesolithic	7700–5000 BC	BLDAM	Hanik, pers. comm.;
Netherlands	Hardinxveld-Giessendam Polderweg	Mesolithic	5500–5000 BC	ROB	Louwe Kooijmans, 2001*a*
Netherlands	Hardinxveld-Giessendam De Bruin	Mesolithic	5500–5000 BC	ROB	Louwe Kooijmans, 2001*b*
Switzerland	Birsmatten-Basisgrotte	Mesolithic	No recent radiocarbon dates	NMBB	Bandi, 1963
Sweden (Gotland)	Ajvide	Middle neolithic	3200–2300 BC	Stock & Got	Burenhult, 1997
Sweden (Gotland)	Ire	Middle neolithic	3200–2300 BC	Hist	Janzon, 1974
Sweden (Gotland)	Grausne	Middle neolithic	3200–2300 BC	Hist	Österholm, 1989
Denmark	Troldebjerg	Middle neolithic	3300 BC	ZMUC	Nielsen, 1998
Germany	Eilsleben	Early neolithic	5500–4900 BC	LVH	Kaufmann, 1983
Germany	Gatersleben	Early neolithic	5500–4900 BC	LVH	Müller, 1959
Netherlands	Swifterbant-S3	Early neolithic	4300–3900 BC	ROB	Raemakers, 1999
France	Bercy	Middle neolithic	No radiocarbon dates	NHMP	Bocherens *et al.*, 1997
France	Villeneuve-Tolosane-Cugnaux	Middle neolithic	No radiocarbon dates	NHMP	Tresset, pers comm.
Switzerland	Seeberg BS	Late neolithic	3800–3700 BC	NMBB	Bandi, 1957–58
Switzerland	Mozart-strasse	Late neolithic	3668–2510 BC	KAZ	Gross-Klee, 1997
Switzerland	Arbon	Late neolithic	3384–3370 BC	AATH	Leuzinger, 2000
Great Britain	Durrington Walls	Late neolithic	2800–2400 BC	Salisbury and Wiltshire Museum	Wainwright & Longworth, 1971
Czech Republic	Homolka	Late neolithic	No recent radiocarbon dates	Peabody Museum Cambridge	Ehrich & Pleslová-Štiková, 1968

Table 3. Numbers of molars from each archaeological assemblage of *Sus scrofa*

Location	No. of M_1	No. of M_2	No. of M_3
Agernæs	4	5	7
Bloksbjerg	5	10	17
Flynderhage	5	3	5
Holmegaard	9	9	9
Kongemose	7	6	11
Lundby	3	3	4
Mullerup	10	1	2
Niva	4	5	12
Norslund	2	2	4
Sludegard	16	15	12
Svaerdborg	1	2	5
Noyen-sur-Seine	4	4	2
Friesack	7	7	14
Hardinxveld-Giessendam Polderweg	12	7	3
Hardinxveld-Giessendam De Bruin	6	6	9
Birsmatten-Basisgrotte	6	3	9
Ajvide	68	73	63
Ire	19	19	4
Grausne	33	31	9
Troldebjerg	54	44	92
Eilsleben	22	17	11
Gatersleben	7	7	3
Swifterbant-S3	15	12	16
Bercy	44	45	32
Villeneuve-Tolosane-Cugnaux	18	19	20
Seeberg BS	95	61	46
Mozart-strasse	163	120	71
Arbon	229	150	110
Durrington Walls	131	64	38
Homolka	46	41	28

them, can cause difficulties distinguishing one form from the other. For the sake of brevity, detailed archaeological descriptions of the individual sites, and of the collected animal remains, will not be presented here. However, a general location for each site is given in Fig. 2.

A full account of the methodology used can be found in Dobney & Ervynck (1998) and Dobney *et al*. (2002). Basically, the presence of individual LEHs were recorded and measured on all separate cusps of the permanent mandibular molars (M_1, M_2 and M_3). Additionally, the crown heights of unworn teeth were measured to take into account possible size differences in the dentition between different *Sus* populations, which could influence the relative position of LEH on the tooth crown. From the LEH measurements, the height distribution of LEH over the crown was established per tooth and cusp. These distributions were transformed using the running mean of three classes in order to reveal trends more clearly. The frequency of LEH within the populations studied was evaluated using the index defined by Ervynck & Dobney (1999):

$$\text{Index}_{(\text{population A})} = \text{average}\left[\frac{F_{(\text{tooth } x,\ \text{cusp } y)\ (\text{population A})}}{F_{(\text{tooth } x,\ \text{cusp } y)\ (\text{all populations})}}\right]$$

with F = number of LEH lines observed/no. of specimens observed, calculated per population, for each individual tooth cusp, when number of specimens > 0. This calculation enables the comparison of the average relative frequency of LEH for a population against that calculated for all populations together (which by definition equals 1). The standard deviation of the calculated average describes the variation between teeth and cusps within a population.

RESULTS

Chronology

To enable comparison of the LEH height distributions between the present-day wild boar populations and those previously published for medieval domestic pigs (Dobney & Ervynck, 2000), the mean crown heights have been established for all recent populations studied here, when the number of observations exceeded five. As an example, Fig. 3 shows the values for the anterior cusp (cusp A) of the M_1, demonstrating that little variation occurs between the wild boar populations. Moreover, the mean crown heights are similar to those established for the medieval pigs (Dobney & Ervynck, 2000; Fig. 3).

Figure 4 shows the LEH height distributions for (as an example) the anterior cusps of the molars of all the recent wild boar populations combined, compared to those of the four medieval domestic pig samples. The similarity between the patterns is striking. The distribution of LEH heights on the M_2 of recent wild boar shows an additional point of interest: a second small peak visible towards the tip of the enamel crown (around 10.5 mm arrowed).

In the mesolithic wild boar populations, the LEH height distribution could not be made for each molar cusp owing to low LEH frequencies (see further), even when all data from the different sites within this period were combined. However, where it was possible (data not presented here), the patterns were similar to those in Fig. 4. Although only few crown heights could be measured from the mesolithic material (data not presented here), the values fell within the variation observed for recent wild boar. When data from all neolithic samples were amalgamated, the height distributions could be made for each molar. Figure 5 shows the graphs for the anterior cusps and illustrates that, despite a wider variation, the patterns are similar to those of the mesolithic and recent wild boar, and to the medieval pigs. The larger variation is certainly partly linked with a larger variation in tooth crown height *between* the neolithic assemblages (Fig. 3). Moreover, also *within* one of the neolithic samples (i.e. all the neolithic material from Switzerland combined, see Fig. 3) the variation in crown height is higher than is the case for the recent wild boar material. One final point worthy of note from the combined neolithic data (Fig. 5) is the small additional peak that can be observed towards the tip of the crown on the M_3.

Frequency

Having established that the chronology of LEH is similar for all the samples under study, the frequency of LEH can

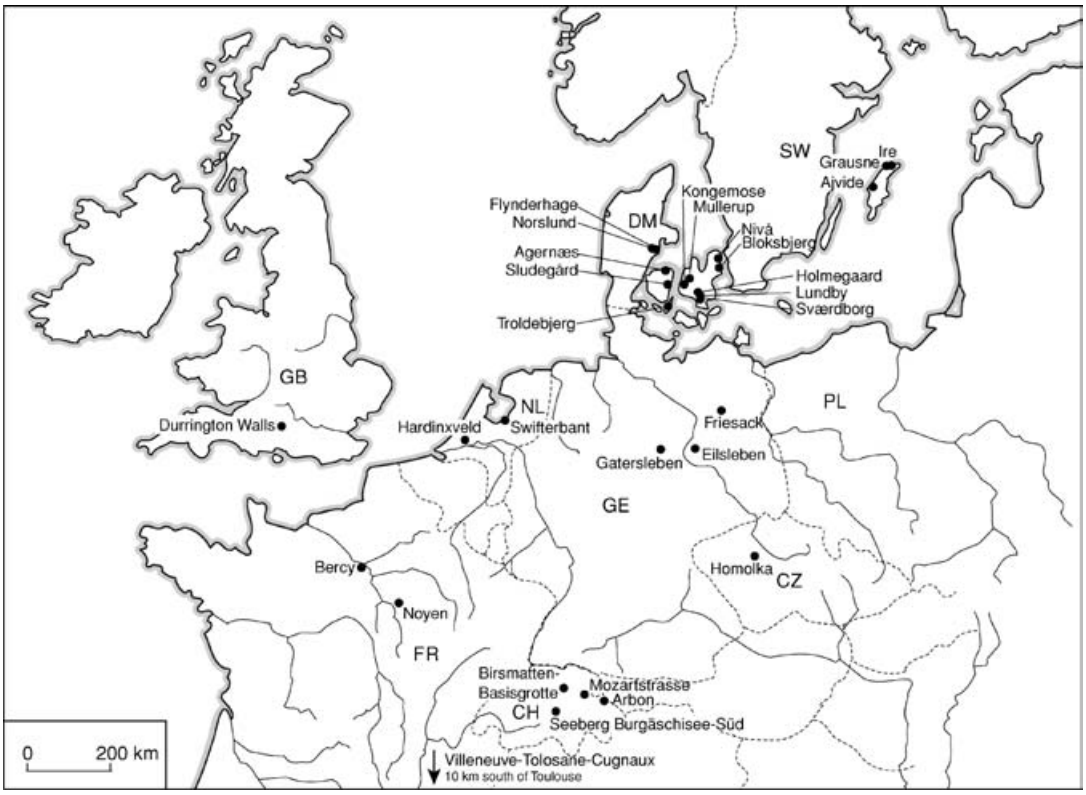

Fig. 2. Location of the archaeological sites used in this study: SW, Sweden; DM, Denmark; GE, Germany; NL, the Netherlands; FR, France; CH, Switzerland; GB, Great Britain; CZ, Czech Republic; PL, Poland.

now be evaluated. For this purpose, in order to obtain sufficiently large datasets, sites have been grouped by main periods (mesolithic, neolithic, recent) and present-day countries. The calculation of the index shows, first of all, that the values for both mesolithic and recent wild boar populations are broadly similar, and (usually) lower than that of the neolithic pigs (Fig. 6). Within the neolithic group, two subsets (i.e. representing Germany and the Netherlands) particularly stand out with values as low as the mesolithic and recent 'wild' populations.

When separate LEH frequencies are calculated per individual molar cusp, once again the low values of the mesolithic and recent wild boar data are highlighted (Fig. 7). Within the mesolithic subgroup (Fig. 7a), a shared pattern seems to be present with low values for M_1, markedly higher values for M_2 and again somewhat lower values for M_3. The higher frequencies within the neolithic samples are the result of a wide variation of increased LEH along the tooth row, without the appearance of a shared pattern (Fig. 7b). The patterns seem to differ between the recent wild boar populations and are not the same as those of the mesolithic wild boar (Fig.7c).

DISCUSSION

The analysis has proven that LEH is not a condition that occurs only in domestic animals. It is obviously a characteristic of wild boar populations, both recent and from the past. Moreover, the chronology of LEH events is the same for both, and for the previously published medieval pig samples (Figs 4 & 5), suggesting that the chronology of events purported as an explanation for those archaeological samples (i.e. physiological stress associated with birth, weaning (M_1) and winter starvation (M_2 and M_3); Dobney & Ervynck, 2000) is also valid for recent wild boar from north-western Europe. Additionally, it is possible that the second small peak in the LEH height distribution for the anterior cusp of the M_2 indicates the occurrence of a smaller second age cohort

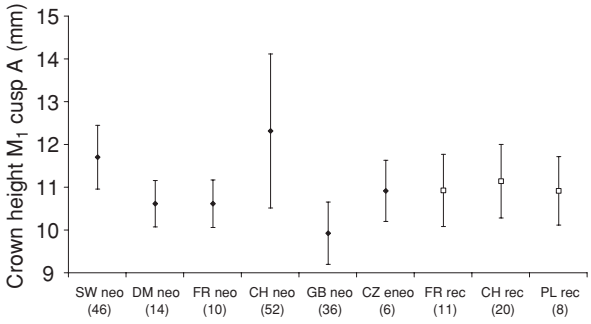

Fig. 3. Average crown height of the anterior cusp of the M_1 established for those assemblages of *Sus scrofa* yielding more than five measurements of unworn teeth. Numbers of observations are given in parentheses. neo, Neolithic domestic pig and possibly wild boar; rec, recent wild boar. For country codes see Fig. 2.

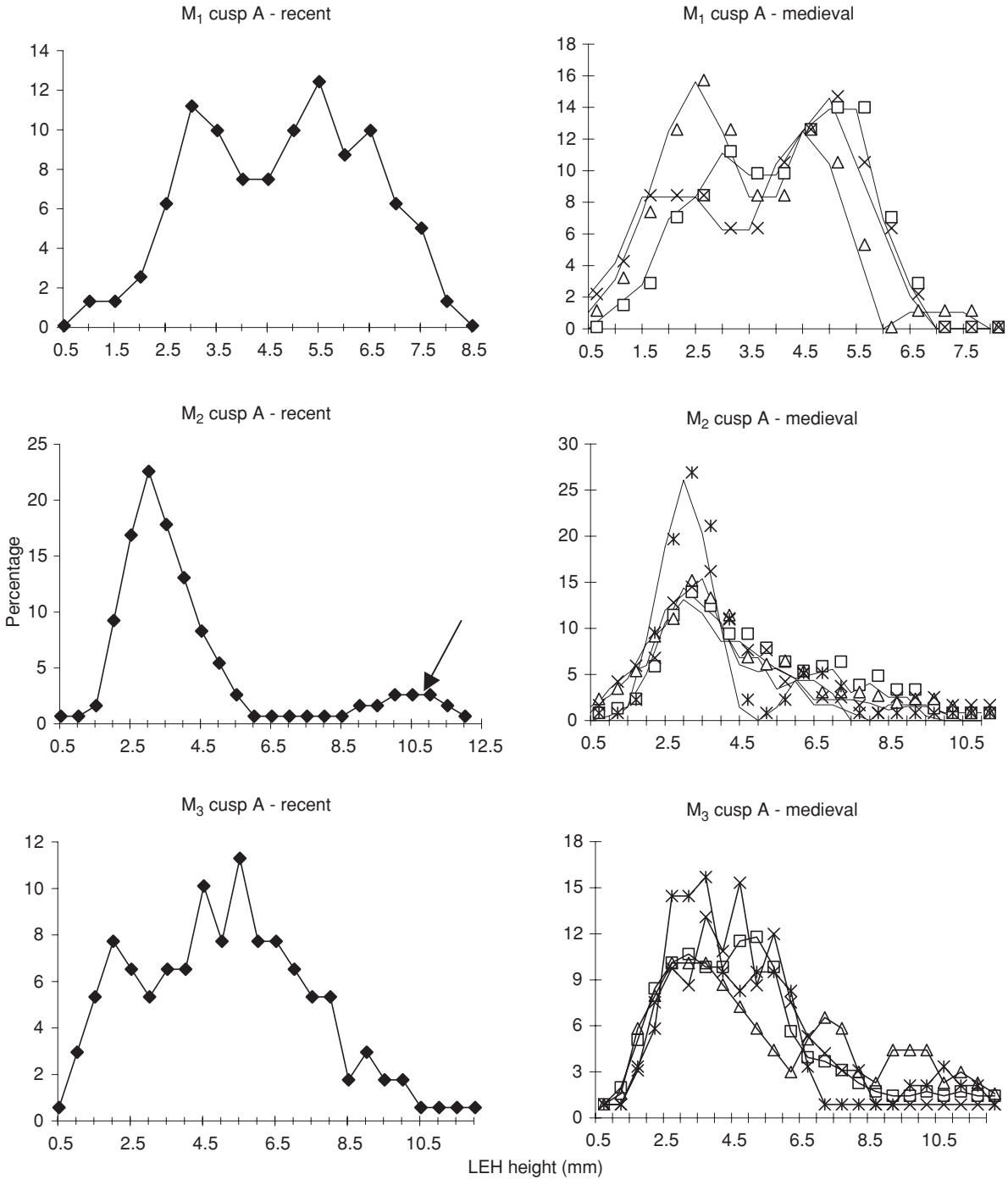

Fig. 4. Frequency distribution of linear enamel hyperplasia (LEH) heights for the anterior cusps of the mandibular molars of recent wild boar *Sus scrofa* (all populations combined; number of observations: M_1, 27; M_2, 35; M_3, 28), compared with that of four previously published medieval assemblages (after Dobney & Ervynck, 2000: fig. 6, see there for number of observations). Arrow, possible effect of second farrowing (see text). M_1, data for the site of Londerzeel were too few to present.

within the population comprising animals born in late summer or early autumn, a pattern well known for European wild boar (Mohr, 1960). The possibility that this second peak represents LEH linked to first winter nutritional deficiencies within an age group characterized by M_2 crowns in their early development (resulting in the 'first winter' LEH event being located higher up the tooth crown) has previously been discussed in detail by Dobney & Ervynck (2000), and also theoretically modelled within an archaeological context (Ervynck & Dobney, 2002). Whether the small peak previously noted in the M_3 of the neolithic material (Fig. 5) could also reflect individuals of a second birth cohort, is impossible to fully assess owing to the wider variation of tooth crown heights found in these assemblages (Fig. 3).

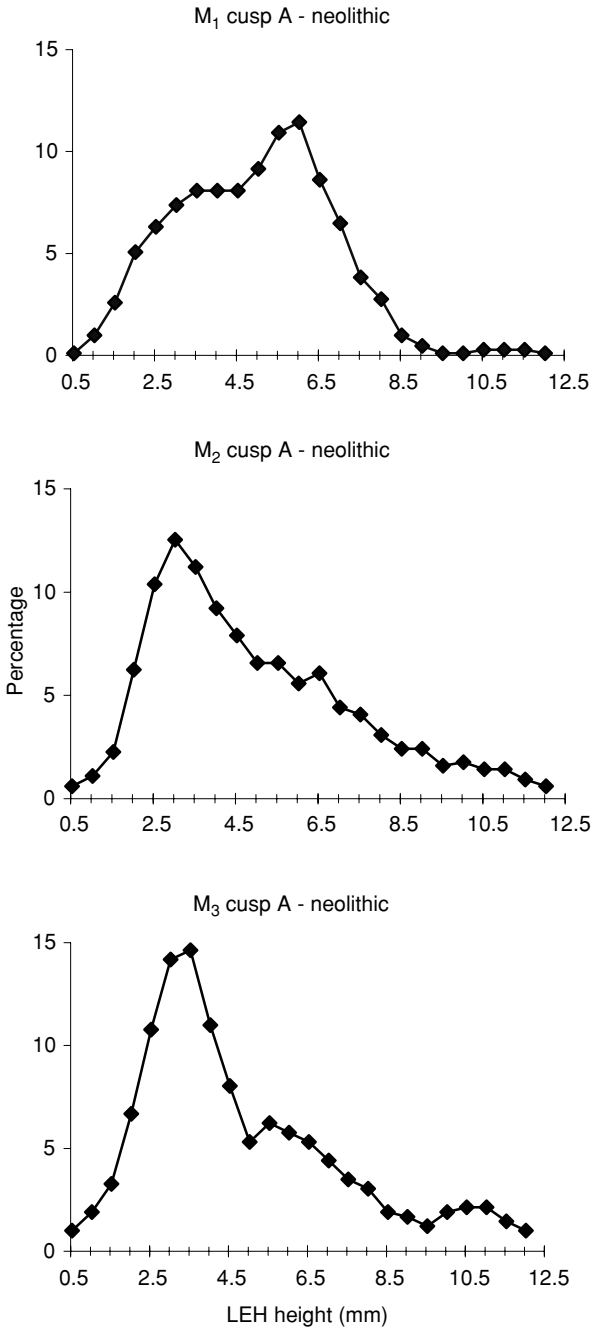

Fig. 5. Frequency distribution of LEH heights for the anterior cusps of the mandibular molars of neolithic *Sus* populations (all neolithic sites combined, number of observations: M_1, 188; M_2, 201; M_3, 147.

In all subsets of wild boar, the LEH frequency seems to be consistently low (Fig. 6). This is true for both the ancient and modern wild boar samples, which are separated by at least 6000 years, and existed under markedly differing living conditions, the result of climatic change, pollution, disturbance, hunting pressure and other forms of human interference. For example, large-scale habitat fragmentation and degeneration has occurred throughout the Holocene, which must have affected the overall fitness of present-day wild boar populations. On the other hand, increased management of wild species in north-western Europe, sometimes including supplementary feeding and veterinary intervention, may have resulted in the converse effect. In this context, it should be noted that it is unclear whether LEH in *Sus* occurs solely as a phenotypic phenomenon, or whether the susceptibility to the condition also has a genetic basis. In the latter case, LEH could be low in wild boar because Darwinian selection acts against it. High LEH frequencies in certain individuals would reflect reduced fitness (certainly when it is invoked by undernourishment), which would have limited their procreative contribution to succeeding generations, resulting in the reduced occurrence of LEH within the population. Following the same reasoning, LEH frequency is high in domestic pig (see further) because natural selection cannot exert its full effect.

Perhaps the most important observations in this study are the differences between the neolithic *Sus* populations and wild boar. Given the fact that the neolithic period immediately succeeds the mesolithic, the observed increase in LEH frequency can be called dramatic. This sudden increase can only be explained as a result of early domestication. Certainly the early domestic pigs herded by the earliest European farming communities must have been subjected to living conditions different to that of their wild conspecifics. Moreover, it must be taken into account that, early in the Neolithic, herds of domestic pigs were probably introduced into north-western Europe from more southern regions (e.g. Benecke, 1994), explaining why the differences between those early domestic animals and the indigenous wild ones can have been so pronounced. On the other hand, free-ranging domestic pigs have always interbred with wild boar, and it has been argued that local domestication attempts could also have occurred (Nobis, 1975; Zvelebil, 1995). In general, the increased physiological stress in the neolithic populations (resulting in higher LEH frequencies) is most likely to have occurred as a result of many phenomena that are part of the complex of animal husbandry. Higher densities of animals, inbreeding, changes in demographic structure from the wild population, and poorly formulated husbandry strategies in general, would have led to the disturbance of the animal's natural behaviour and feeding regimes (Price, 1984). As a result, a rise in pathological conditions such as LEH would have been a consequence of early domestication. The same conclusion has been drawn for the Turkish site of Çayönü Tepesi, one of the earliest purported sites for pig domestication in western Eurasia (Ervynck *et al*., 2001).

Although we have established that the LEH frequency is generally higher within the neolithic group of samples, there is interesting variation between the individual datasets, which could highlight differences between sites or cultures, or between phases within the neolithic (where the terms 'early', 'middle' or 'late' are used, these refer to the local chronologies, which can differ markedly between regions within Europe). The highest index values are from the Swedish, Danish, French and British material. In the Danish and British samples, derived from the middle

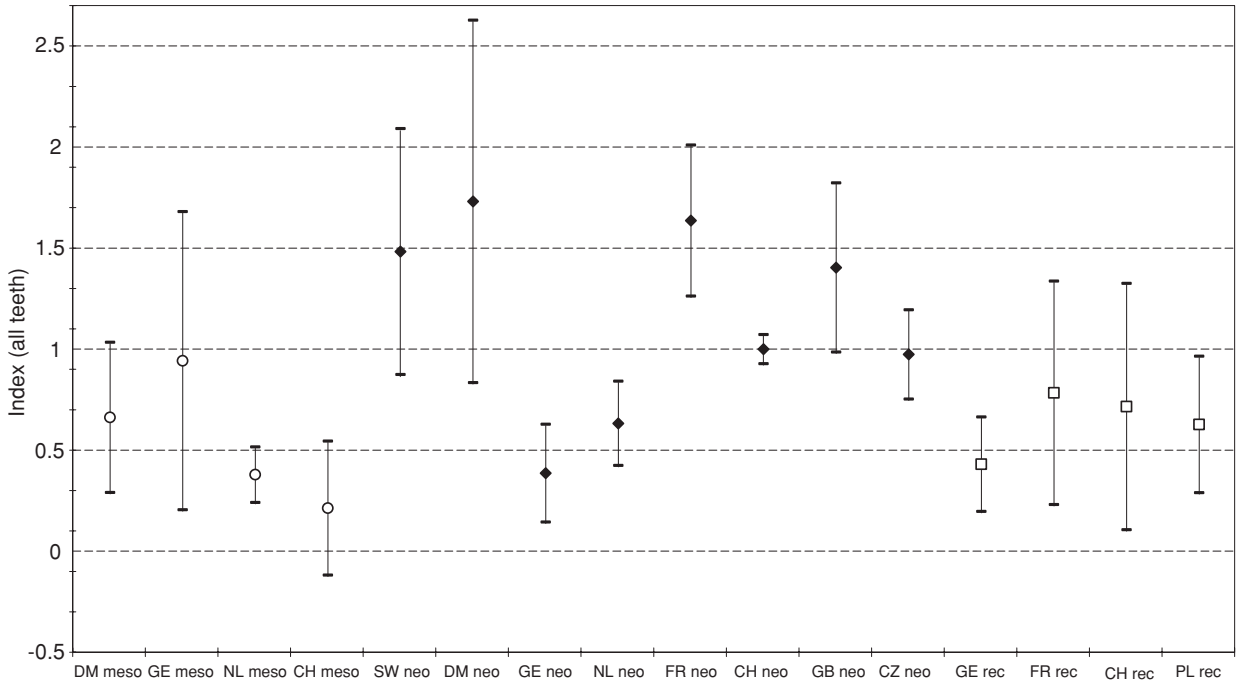

Fig. 6. Index comparing the average frequency of linear enamel hyperplasia between the *Sus* populations studied. Error bars are calculated as mean ± SD: meso, mesolithic wild boar; neo, neolithic domestic pig and possibly wild boar; rec, recent wild boar. For country codes see Fig. 2; for sample sizes see Tables 1 & 2. FR meso has been omitted because of the small number of observations).

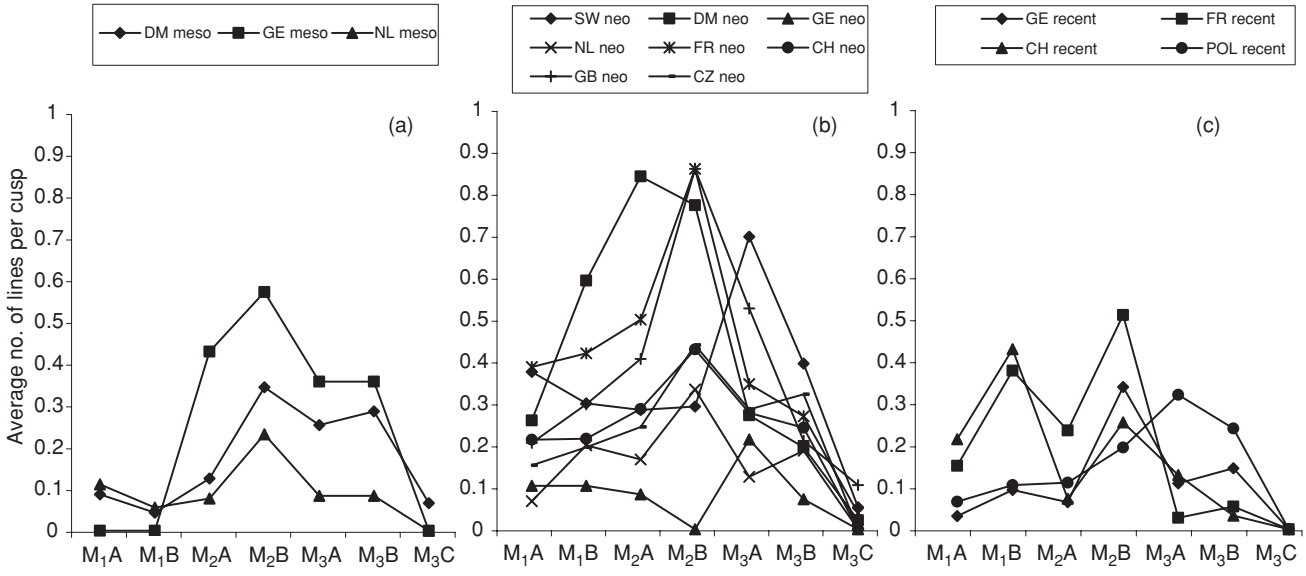

Fig. 7. Average number of lines recorded per molar cusp, for all *Sus* populations: (a) mesolithic; (b) neolithic; (c) recent. See Figs 2 & 6 for codes. For sample sizes see Tables 1 & 2. FR meso and CH meso have been omitted because of small number of observations.

neolithic site of Troldebjerg (*c*. 3300 BC; Nielsen, 1998) and the late neolithic henge monument of Durrington Walls (2800–2400 BC: Wainwright & Longworth, 1971), the biometrical data leave no doubt about the domestic status of the pigs (Higham, 1967; Albarella & Serjeantson, 2002). The Swedish dataset represents three middle neolithic sites, all from the island of Gotland in the southern Balthic (i.e. Ajvide, Ire and Grausne, 3200–2300 BC; Burenhult, 1997; Österholm, 1989), but unlike the Danish material, there is still much debate about the actual status of the *Sus* remains, even though they were certainly introduced by humans (Jonsson, 1986). Biometry has been used to argue that they were either domestic (Benecke, 1994) or wild (Rowley-Conwy & Storå, 1997), that is feral or even introduced as wild. Our data could tentatively suggest that the 'domestic' hypothesis is the most likely, although the effects of a small island ecosystem could also have played a part. The neolithic French data derive from

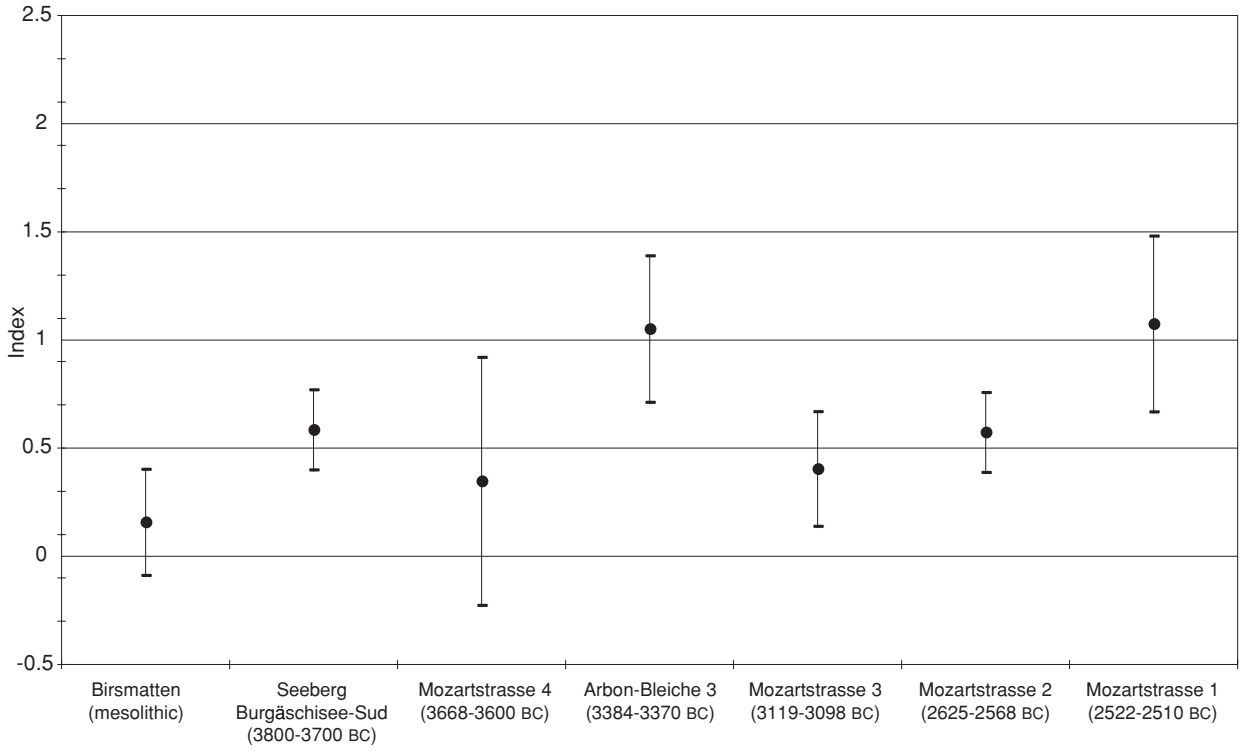

Fig. 8. Index comparing the average frequency of linear enamel hyperplasia between the mesolithic (Birsmatten) and neolithic (Arbon, Mozartstrasse, Seeberg) *Sus* populations from Switzerland. Error bars calculated as mean ± SD. For sample sizes see Table 2.

two contemporary assemblages of middle neolithic date (*c*. 4000 BC) representing the Chasséen culture. The first assemblage is from the site of Bercy from the Paris basin, the second the site of Villeneuve-Tolosane-Cugneux near Toulouse. Although analysis of the fauna from both sites is still unpublished, preliminary work indicates the presence of both wild boar and domestic pigs in both these assemblages, in roughly equal proportions (A. Tresset, pers. comm.). When wild animals were still important within the *Sus* population, the high value for the LEH index remains surprising. However, there is also a major difference between the separate index values for the sites, with an especially high value for Bercy, in fact the highest for all neolithic sites in our study (data not represented here). How these patterns can be explained is not clear, but most probably varying ecological conditions for the sites must have played a role. Not only would different regions have provided widely varying foraging conditions for *Sus*, but forest clearance (or other anthropogenic changes affecting vegetation cover and general food availability) would have progressed at different rates and scales across Europe in the past.

In contrast to the neolithic assemblages already discussed, material from Switzerland and the Czech Republic shows lower index values (Fig. 6). Of course, both these datasets are from central Europe where a more continental climate and large expanses of forest cover perhaps provided optimal conditions for wild boar. Additionally, domestic pigs in these areas could well have enjoyed comparable living conditions to those of wild boar (i.e. free-ranging foraging with very limited human interference). To investigate this further, the large Swiss dataset (both mesolithic and neolithic) has been analysed by individual site and, for the stratified site of Zürich-Mozartstrasse, by layer (Fig. 8). This shows that significant variation exists between the sites and diachronic samples, tentatively showing a trend towards higher index values through time. This could, for example, suggest a gradual intensification of pig husbandry (see Schibler, Hüster-Plogmann *et al*., 1997; Schibler, 1997 for a discussion of this interpretation), although it remains equally probable that varying proportions of wild boar *vs* domestic pig amongst the *Sus* remains are responsible for the trend. Birsmatten is a mesolithic site (no finer dating available; Bandi, 1963) in which no domestic pigs occurred (Schmid, 1963) while at Seeberg, a site that is neolithic in date (3800–3700 BC: Bandi, 1957–58), a very high frequency of hunted species occurred (82 to 94%: Boessneck, Jéquier & Stampfli, 1963), making it very probable that a significant part of the *Sus* remains represents wild animals. This assumption has been corroborated by further biometric analysis of the material by Payne & Bull (1988; Fig. 8), although in this latter paper it is suggested that the frequency of wild specimens may not have been as high as originally purported.

Considering the site of Zürich-Mozartstrasse, only the material from three of the neolithic layers (4, 3 and 2, 3668–2510 BC; Gross-Klee, 1997) yielded enough material to be discussed here. It has been observed that the overall percentage of wild boar within the *Sus* population declines from 62% in layer 4, over 11% in layer 3 to 5% in layer 2. This percentage is even

further reduced to 2% when Bronze Age layer 1 is taken into account (Hüster-Plogmann & Schibler, 1997: tables D66–D75), possibly explaining the gradually higher index values, and thus again suggesting that an increase of LEH frequency is a characteristic signature of early domestication. Intriguingly, the fourth millennium BC site of Arbon (Leuzinger, 2000) shows an LEH index value that is higher than that of the slightly older population of Mozartstrasse 4 and of the slightly younger group from Mozartstrasse 3 (Fig. 8). It is difficult to establish whether this pattern is related with higher frequencies of domestic pig at the Arbon site, but the possibility cannot be excluded. At present, the proportion of wild boar amongst the *Sus* remains has been estimated at *c*. 20% (Deschler-Erb, Marti-Grädel & Schibler, 2002). More importantly, it is perhaps more than coincidence that within the current framework of understanding, the Arbon site represents the first neolithic settlement in Switzerland concentrating specifically on pigs within their animal husbandry strategy (J. Schibler, pers. comm.). Perhaps this high density within pig herds resulted in increased levels of physiological stress?

In contrast to those sites already discussed, the lowest values for the neolithic sites studied are from the German Linear Bandkeramic (LBK) sites of Eilsleben (5500–4900 BC; Kaufmann, 1983) and Gatersleben (5500–4900 BC; Müller, 1959), and from the Dutch site of Swifterbant–S3 (4300–3900 BC; Raemakers, 1999). The Linear Bandkeramic culture represents the first farming communities within Germany although, in some instances, hunting remained an important factor within the food economy (Whittle, 1996; Arbogast, Jeunesse & Schibler, 2001). Archaeozoological research concluded on osteometric grounds that domestic pig outnumbered wild boar at both German sites (Müller, 1964; Döhle, 1994). In general, however, pig breeding remained unimportant within the Linear Bandkeramic culture (in contrast to cattle herding), an observation which even raised the question whether all *Sus* remains at LBK sites should not be regarded as coming from wild animals (Kaufmann, 1983). Finally, the contribution of crop growing and herding to the different phases within the Swifterbant culture, known from the area bordering the southern North Sea, from northern Flanders to northern Germany, is still much debated (Raemaekers, 1999). Previous study of the bones from the S3 site made no distinction between the remains of wild boar and domestic pig (Zeiler, 1997). Thus, the Swifterbant material studied for LEH may derive for an important part from hunted wild boar, a statement possibly corroborated by the low frequency of LEH, comparable to that in the mesolithic and recent wild boar samples.

CONCLUSION

This study demonstrates that LEH occurs in recent and ancient northwest-European wild boar populations, and that the occurrence of the condition can be explained by the same events within the animal's life (birth, weaning, winter starvation) as has been previously suggested for archaeological domestic pig samples. Moreover, the frequency of this dental defect is consistently low within all ancient and recent populations of wild boar studied. In contrast, early domestic populations show generally higher LEH frequencies, although considerable variation exists between the samples. This variation must be related to differences in husbandry regimes and ecological conditions, and to the varying proportions of wild boar amongst the *Sus* remains recovered from the sites, although this last statement cannot be proven for each site, given the difficulties in discriminating wild boar and domestic pig on osteometric grounds. In general, it can be concluded that higher frequencies of LEH in ancient pig populations can be broadly explained by direct or indirect human interference in the form of domestication and husbandry. This conclusion indicates that the observation of LEH therefore provides zooarchaeologists with a valuable additional tool for studying the processes of early pig domestication and husbandry.

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REFERENCES

Aaris-Sørensen, K. (1988). *Danmarks forhistoriske dyreverden.* Copenhagen: Gyldendal.

Albarella, U. & Serjeantson, D. (2002). A passion for pork. Meat consumption at the British Late Neolithic site of Durrington Walls. In *Consuming passions and patterns of consumption:* 33–49. Miracle, P. & Milner, N. (Eds). Cambridge: McDonald Institute for Archaeological Research.

Arbogast, R.-M., Jeunesse, C. & Schibler, J. (2001). *Rôle et statut de la chasse dans le Néolithique ancien danubien (5500–4900 av. J.-C.)/Rolle und Bedeutung der Jagd während des Frühneolithikums Mitteleuropas (Linearbandkeramik 5500–4900 v.Chr.). Premières rencontres danubiennes, Strasbourg 20 et 21 novembre 1996, Actes de la première table-ronde (Internationale Archäologie: Arbeitsgemeinschaft, Symposium, Tagung, Kongress Band 1)*. Rahden/Westfalia: Marie Leidorf.

Bandi, H.-G. (1957/58). Die jungsteinzeitliche Ufersiedlung Seeberg/Burgäschisee-Süd. *Jahrb. Hist. Mus. Bern* **37/38**: 197–205.

Bandi, H.-G. (1963). *Birsmatten – Basisgrotte. Ein mittelsteinzeitliche Fundstelle im unteren Birstal. (Acta Bernensia I)*. Bern: Verlag Stämpfli.

Benecke, N. (1994). *Der Mensch und seine Haustiere. Die Geschichte einer jahrtausendealten Beziehung*. Stuttgart: Theiss.

Bocherons, H., Tresset, A., Wiedemann, F., Giligny, F., Lafage, F., Lanchon, Y. & Mariotti, A. (1997). Diagenetic evolution of mammal bones in two French Neolithic sites. *Bull. Soc. Géol. Fr.* **5**: 555–564.

Boessneck, J., Jéquier, J.-P. & Stampfli, H.-R. (1963). *Seeberg Burgäschisee-Sud. Die Tierreste (Acta Bernensia 3).* Bern: Verlag Stämpfli.

Burenhult, G. (1997). *Ajvide och den Moderna Arkeologin*. Falköping: Natur och Kultur.

Colyer, F. (1936). *Variations and diseases of the teeth of animals*. London: John Bale, Sons and Danielson.

Deschler-Erb, S., Marti-Grädel, E. & Schibler, J. (2002). Die Knochen, Zahn- und Geweihartefakte. In *Die jungsteinzeitliche Seeufersiedlung Arbon/Bleiche 3. Funde (Archäologie im Thurgau 11)*: 277–366. de Capitani, A., Deschler-Erb, S., Leuzinger, U., Marti-Grädel, E. & Schibler, J. (Eds). Thurgau: Departement für Erziehung und Kultur.

Dobney, K. & Ervynck, A. (1998). A protocol for recording enamel hypoplasia on archaeological pig teeth. *Int. J. Osteoarchaeol*. **8**(4): 263–274.

Dobney, K. & Ervynck, A. (2000). Interpreting developmental stress in archaeological pigs: the chronology of linear enamel hypoplasia. *J. archaeol. Sci*. **27**(7): 597–607.

Dobney, K., Ervynck, A. & La Ferla (2002). Assessment and further development of the recording and interpretation of linear enamel hypoplasia in archaeological pig populations. *Environ. Archaeol*. **7**: 35–46.

Döhle, H.-J. (1994). *Die Linienbandkeramischen Tierknochen von Eilsleben, Bördekreis. Ein Beitrag zur neolithischen Haustierhaltung und Jagd in Mitteleuropa (Veröffentlichungen des Landesamtes für Archäologische Denkmalpflege Sachsen-Anhalt 47)*. Halle: Landesamt für Archäologie Sachsen-Anhalt.

Ehrich, R. W. & Pleslová-Štiková, E. (1968). *Homolka. An eneolithic site in Bohemia*. Cambridge, MA: Peabody Museum.

Ervynck, A. & Dobney, K. (1999). Lining up on the M_1: a tooth defect as a bio-indicator for environment and husbandry in ancient pigs. *Environ. Archaeol*. **4**: 1–8.

Ervynck, A. & Dobney, K. (2002). A pig for all seasons? Approaches to the assessment of second farrowing in archaeological pig populations. *Archaeofauna* **11**: 7–22.

Ervynck, A., Dobney, K., Hongo, H. & Meadow, R. (2001). Born free? New evidence for the status of *Sus scrofa* at Neolithic Çayönü Tepesi (Southeastern Anatolia, Turkey). *Paléorient* **27**(2): 47–73.

Goodman, A. H., Brooke-Thomas, R., Swedland, A. C. & Armelagos, G. J. (1988). Biocultural perspectives on stress in prehistoric, historical and contemporary population research. *Yearb. phys. Anthropol*. **31**: 169–202.

Gross-Klee, E. (1997). Einleitung. In *Ökonomie und Ökologie neolithischer und bronzezeitlicher Ufersiedlungen am Zürichsee:* 13–39. Schibler, J., Hüster-Plogmann, H., Jacomet, S., Brombacher, C., Gross-Klee, E. & Rast-Eicher, A. (Eds). Zürich: Kanton Zürich.

Higham, C. F. W. (1967). Stock rearing as a cultural factor in prehistoric Europe. *Proc. Prehist. Soc*. **33**: 84–106.

Hüster-Plogmann, H. & Schibler, J. (1997). Archäozoologi.e. In *Ökonomie und Ökologie neolithischer und bronzezeitlicher Ufersiedlungen am Zürichsee:* 40–121. Schibler, J., Hüster-Plogmann, H., Jacomet, S., Brombacher, C., Gross-Klee, E. & Rast-Eicher, A. (Eds). Zürich: Kanton Zürich.

Janzon, G. (1974). *Gotlands Mellanneolitiska gravar (Studies in North European archaeology* **6***)*. Stockholm: Almqvist & Wiksell.

Johansen, A. D. (2000). *Ældre Stenalder i Norden*. Farum: Sammenslutningen af Danske Amatørarkæologer.

Jonsson, L. (1986). From wild boar to domestic pig – a reassessment of neolithic swine of north-western Europe. In *Nordic late quaternary biology and ecology* (*Striae* **24**): 125–129. Königsson, L.-K. (Ed.). Uppsala: University of Uppsala.

Kaufmann, D. (1983). Die ältestlinienbandkeramischen Funde von Eilsleben, Kr. Wanzleben, und der Beginn des Neolithikums om Mittelelbe-Saale-Gebiet. *Nachr. Niedersach. Urgesch.* **52**: 177–202.

Leuzinger, U. (2000). *Die jungsteinzeitliche Seeufersiedlung Arbon-Bleiche 3. Befunde (Archäologie im Thurgau 6)*. Frauenfeld: Veröffentlichungen des Amtes für Archäologie des Kantons Thurgau.

Louwe Kooijmans, L. P. (2001*a*). *Hardinxveld-Giessendam Polderwe.g. Een mesolithisch jachtkamp in het rivierengebied (5500–5000 v.Chr.) (Rapportage Archeologische Monumentenzorg 83)*. Amersfoort: Rijksdienst voor het Oudheidkundig Bodemonderzoek.

Louwe Kooijmans, L. P. (2001*b*). *Hardinxveld-Giessendam De Bruin. Een kampplaats uit het Laat-Mesolithicum en het begin van de Swifterbant-cultuur (5500–4450 v.Chr.) (Rapportage Archeologische Monumentenzorg 88)*. Amersfoort: Rijksdienst voor het Oudheidkundig Bodemonderzoek.

Marinval-Vigne, M.-C., Mordant, D., Auboire, G., Augereau, A., Bailon, S., Dauphin, C., Delibrias, G., Krier, V., Leclerc, A.-S., Leroyer, C., Marinval, P., Mordant, C., Rodriguez, P., Vilette, P. &Vigne, J.-D. (1989). Noyen-sur Seine, site stratigrafié en milieu fluviatile: une étude multidisciplinaire intégrée. *Bull. Soc. Prehist. Fr.* **10**(12): 370–379

Mohr, E. (1960). *Wilde schweine*. Wittenberg Lutherstadt: A. Ziemsen.

Müller, H.-H. (1959). Ausgrabungen vorgeschichtlicher Funde im Gelände des Institutes für Kulturpflanzenforschung in Gatersleben. *Kulturpflanze* **7**: 55–72.

Müller, H.-H. (1964). *Die Haustiere der mitteldeutschen Bandkeramiker (Schriften der Sektion für Vor und Frühgeschichte 17)*. Berlin: Akademie der Wissenschaften.

Nielsen, P. O. (1998). De ældste langhuse. Fra toskibet til treskiber huse I Norden. *Bebyggelseshist. Tidsskr*. **33**: 9–30.

Nobis, G. (1975). Zur Fauna des ellerbekzeitlichen Wohnplatzes Rosenhof in Ostholstein I. *Schr. Naturwissensch. Vereins Schleswig-Holstein* **45**: 5–30.

Noe-Nygaard, N. & Richter, J. (1990). Seventeen wild boar mandibles from Sludegårds Sømose – offal or sacrifice? In *Experimentation and reconstruction in environmental archaeology:* 175–189. Robinson, D. E. (Ed.). Oxford: Oxbow Books.

Noe-Nygaard, N. & Richter, J. (In press). Agernæs. *Acta Archaeol.*

Österholm, I. (1989). *Bosättningsmönstret på Gotland under Stenåldern (Theses and papers in archaeology 3)*. Stockholm: Institute of Archaeology.

Payne, S. & Bull, G. (1988). Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *Archaeozoologia* **2**(1/2): 27–66.

Price, E. O. (1984). Behavioral aspects of animal domestication. *Q. Rev. Biol*. **59**(1): 1–32.

Raemaekers, D. C. M. (1999). *The articulation of a 'new neolithic'. The meaning of the Swifterbant Culture for the process of neolithisation in the western part of the North European Plain (4900–3400* BC*) (Archaeological Studies Leiden University 3)*. Leiden: Faculty of Archaeology, University of Leiden.

Rowley-Conwy, P. & Storå, J. (1997). Pitted Ware seals and pigs from Ajvide, Gotland: methods of study and first results. In *Remote sensing* **I** *(Theses and papers in North European archaeology 13a)*: 113–127. Burenhult, G. (Ed.). Stockholm: Institute of Archaeology, University of Stockholm.

Sarnat, H. & Moss, S. J. (1985). Diagnosis of enamel defects. *NY State Dental J.* **51**(2), 103–106.

Schibler, J. (1997). Haus- und Wildtiernutzung in der jungsteinzeitlichen Feuchtbodensiedlungen des Kantons Thurgau. *Archäol. Schweiz* **20**: 57–61.

Schibler, J., Hüster-Plogmann, H., Jacomet, S., Brombacher, C., Gross-Klee, E. & Rast-Eicher, A. (1997). *Ökonomie und Ökologie neolithischer und bronzezeitlicher Ufersiedlungen am Zürichsee*. Zürich: Kanton Zürich.

Schibler, J., Jacomet, S., Hüster-Plogmann, H. & Brombacher, Ch. (1997). Economic crash in the 37th and 36th century bc cal in neolithic lake shore sites in Switzerland. *Anthropozoologica* **25–26**: 553–570.

Schmid, E. (1963). Die Tierknochen. In *Birsmatten-Basisgrotte. Ein mittelsteinzeitliche Fundstelle in unteren Birstal (Acta Bernensia I)*: 93–100. Bandi, H.-G. (Ed.). Bern: Verlag Stämpfli.

Wainwright, G. J. & Longworth, I. H. (1971). *Durrington Walls: excavations 1966–1968.* London: Society of Antiquaries.

Whittle, A. (1996). *Europe in the neolithic. The creation of new worlds*. Cambridge: Cambridge University Press.

Zeiler, J. T. (1997). *Hunting, fowling and stock-breeding at neolithic sites in the western and central Netherlands*. Unpublished PhD thesis, University of Groningen.

Zvelebil, M. (1995). Hunting, gathering, or husbandry? Management of food resources by the late Mesolithic communities of temperate Europe. *MASCA Res. Pap. Sci. Archaeol*. **12**(Suppl.): 79–104.